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A Biographical Memoir by
DAN ARP AND DAVID DALTON

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Biographical Memoir

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Harold Evans

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BY DAN ARP AND DAVID DALTON

HAROLD J. EVANS WAS A PIONEER AND WORLD LEADER in the study of mineral nutrition in plants and bacteria with a particular interest in minerals required in only small amounts. His interest in mineral nutrition was coupled with an interest in how plants obtain nitrogen for growth. Following these two interests, he demonstrated a role for molybdenum in plants in general and in nitrate reductase specifically. He demonstrated a role for cobalt in legumes, which was confined to their symbiotic growth with a nitrogen-fixing bacterium. He laid the groundwork for understanding how plants, working in a symbiosis with rhizobia bacteria, utilize nitrogen in the air as a source of nitrogen for growth. He demonstrated the significance of a system to recycle hydrogen produced by nitrogenase during the process of nitrogen fixation; the recycling system required two more trace elements, nickel and selenium. He was known for his scientific rigor and tenacity. He had the rare ability to understand and approach a problem from different levels and rapidly adopt and develop new technologies to apply to current problems.

Harold J. Evans was born on February 19, 1921. He grew up on a farm just outside Woodburn, Kentucky, near Franklin, Kentucky. His father was James H. Evans, and his mother was Allie (Uhls) Evans. Harold was the eldest son of seven

children. The family raised tobacco on their small farm. While growing up on the farm, Harold gained an appreciation for hard work and the importance of utilizing the land wisely. These lessons would have a dramatic influence on his career. He became involved in 4-H at an early age. The connection of 4-H to the Kentucky Agricultural Extension program steered Harold toward a college education. Harold entered the University of Kentucky in Lexington with 12 dollars given to him by his mother. He supported himself working as a newsboy and dishwasher. The University of Kentucky provided him with the support and flexibility he needed to complete his bachelor's degree.

At the age of 22 Harold made the decision to place his education on hold when he enlisted in the U.S. Army. The year was 1943, and World War II was at a critical point. Harold became a medic and was stationed in New Guinea, the Philippines, and Australia. It was in Australia—on R&R leave and on the dance floor—that Harold met his future wife, Elizabeth Mavis Dunn. Mavis served in the Australian army with the Australian Signal Corp. Harold returned to Kentucky after the war and resumed his studies. But he continued to correspond with Mavis and eventually asked her to be his wife. On December 14, 1946, they were married in Lexington, Kentucky. Clearly, the war had a profound effect on this young man, as it also did on Mavis.

In the spring of 1946, Harold completed his undergraduate studies earning the B.S. degree. He continued with his education at the University of Kentucky in Lexington and two years later completed his M.S. degree. He and Mavis moved to Rutgers University in New Brunswick, New Jersey, in 1948 to begin work on his Ph.D. Shortly thereafter, their first daughter, Heather, was born. Remarkably, in just two years Harold had earned his Ph.D.—with adviser E. R. Purvis. Harold's interest in mineral nutrition in plants took root at

Rutgers and continued throughout the next 40 years of his professional career.

Following completion of his Ph.D., Harold accepted a position as an assistant professor of soil science at North Carolina State University. A short time later he accepted an E. F. Johnson Post-doctoral Fellowship in biochemistry at Johns Hopkins University, working with Alvin Nason. Evans and Nason provided some of the first characterizations of the plant enzyme (in their case from soybeans), nitrate reductase, which initiates the reduction of nitrate by plants. While Harold's M.S. and Ph.D. work had included studies of whole plants in field trials, this fellowship provided Harold with the opportunity to advance his interests to include studies at the protein level. Harold was becoming a plant biochemist, and his work was being recognized by other plant biochemists of note at that time. This became a hallmark of Harold's scientific contributions—an uncanny ability to bring together a new technology or approach with a pressing problem to produce rapid advances in the field.

In 1952 Harold returned from his fellowship at Johns Hopkins to North Carolina State University, but now as an assistant professor of botany. The same year, Harold's second daughter, Pamela, was born. Harold continued at North Carolina State University for the next nine years, having been promoted to associate professor and professor of botany. Harold was always proud of the fact that from his humble beginnings on a tobacco farm in Kentucky he was promoted to professor at a major research university by the age of 37.

In 1961 Harold moved the family west to Corvallis, Oregon, where Harold had accepted a position as professor in the Botany and Plant Pathology Department at Oregon State University. The move required some adjustment for the family—the weather, the culture, and the size of the

city were all markedly different from what the family had become accustomed to in Raleigh. The family lived close to local schools and the campus of Oregon State University, with downtown only a few blocks farther away. Harold was a professor of plant physiology at Oregon State until his retirement in 1989. Of course, he did not stand still during those 18 years. As his work became increasingly molecular over the years, he became an affiliate professor of biochemistry in 1968. Though botany and plant pathology was home to many prestigious and productive plant scientists, Harold quickly became the best known, best funded, and most productive professor.

By the mid-1970s Harold became concerned that the returned overhead generated by his grants was not being used wisely by the department. He sought independence from the department, and his research program was established in 1978 as an independently organized research unit in the College of Agricultural Sciences and Oregon Agricultural Experiment Station. The unit was named the Laboratory for Nitrogen Fixation Research, and Harold was the director until his retirement in 1989. During its peak years, the Laboratory for Nitrogen Fixation Research was one of the more productive laboratories in the world in the field of nitrogen fixation. The laboratory attracted graduate students, postdoctoral associates, and visiting scientists from across the country and the world. Under Harold's direction the laboratory was well known for its ability to attack a problem from a variety of approaches. It was not uncommon to have field and greenhouse components combined with enzyme studies and genetic and molecular biological approaches to study a problem.

The Rockefeller Foundation supported Harold as a visiting professor at the University of Sussex in 1969. During that time, Harold's friendship with John Postgate deepened.

Postgate was another luminary in the rapidly growing field of nitrogen fixation, and they stayed in touch throughout each other's careers. Harold also formed a deep friendship with Robert Burris at the University of Wisconsin. Burris, another leader in the field of nitrogen fixation, and Evans were among the handful of scientists at the first workshop of scientists working in the field of nitrogen fixation. Out of that meeting grew the Nitrogen Fixation Congress series that routinely attracted 400-600 scientists. Burris and Evans were regular attendees at these and other meetings. Their wives, Mavis and Katherine, also grew to be good friends as they accompanied their husbands to the more attractive and exotic meeting locations. Many students who got their start in Burris's laboratory would move on to Harold's laboratory for their postdoctoral studies. And the converse was also often the case, that is, students who completed studies in Harold's laboratory would then move to the Burris laboratory to further their studies in nitrogen fixation.

Harold received many awards over the years, both from Oregon State University and from national organizations. One of the earliest national awards was the 1964 Hoblitzelle National Award for his work on cobalt requirements of legumes and rhizobia. He received many awards at Oregon State for his research accomplishments. In 1988 Oregon State established a program to recognize two professors each year for their excellent scholarship, teaching, and outreach. Harold was one of the inaugural recipients of this prestigious local award. He carried the title of Distinguished Professor until his retirement in 1989, when he became Distinguished Professor Emeritus. But without a doubt Harold was most proud of his election to the National Academy of Sciences, in 1972. He was the first individual at Oregon State University to be elected to the Academy. Harold was also very proud

of the fact that he received uninterrupted support from the National Science Foundation for 32 years.

During their time at the University of Kentucky, Rutgers, Johns Hopkins, North Carolina State University, and Oregon State University, Mavis remained the loyal and devoted wife. She focused on raising the family while Harold focused on his science. Mavis was a wonderful host to all the scientists and their families who passed through Harold's laboratory. She hosted frequent parties at her house, took visitors out to dinners, and led tours of Corvallis. She helped get families established and she always seemed to have one more set of used dishes to share or knew someone with an extra bed to get rid of. She seemed to satisfy some of her own wanderlust by getting to know these people, who came from all across the country. And she was the source of all information about Corvallis and Oregon that did not involve the university. She was always welcoming and friendly and one immediately felt at ease when with Mavis. A warm and gracious host, Mavis was also known for her sharp wit. Harold was often the subject of her humorous stories, a role that he seemed to accept willingly, perhaps in acknowledgement of his good fortune of having met Mavis on that dance floor back in Australia during World War II.

In spite of her warm personality and her amazing ability to support the people who worked with Harold, Mavis had absolutely no interest in the science that brought these people together. None. Zero. And even less interest in the politics at the university. At a party even a simple question like "How did your experiment work out?" if overheard by Mavis was enough to earn one of her famous "They're talking about the laboratory again. I don't give a damn about science or what goes on in that laboratory." And she managed to keep the science cordoned off for all of Harold's career. As he approached retirement, this became somewhat of a point of

pride for both of them. Mavis would point out that in 28 years, she had never been in Cordley Hall, where the laboratory was located. Harold would then remind Mavis of the one time she was in Cordley to drop off a visitor. It never seemed to be resolved whether the drop-off occurred in the lobby on the first floor or in the hallway on the fourth floor where the laboratory was located. But both agreed that Mavis had never stepped foot in either Harold's office or the laboratory. In 1990 at the Eighth International Nitrogen Fixation Congress held in Knoxville, Tennessee (May 20-26, 1990), Harold was honored for a lifetime of scientific contributions. One of us (D.A.) gave the talk recognizing Harold's contributions, and Mavis was in attendance. The talk included slides with views of the inside of Harold's laboratory as well as his office. After the talk, Mavis confirmed that was indeed the first time that she had seen the inside of either Harold's office or his laboratory.

It is perhaps not surprising then that upon Harold's retirement, he gave Mavis the choice in where they would live next. Though she enjoyed her time in Corvallis, Mavis was now ready to spend her retirement years in a big city. She chose Lake Oswego, a suburb of Portland, Oregon. Not at all coincidentally, her two daughters and their families also lived in the Portland area. Harold and Mavis lived together in Lake Oswego until Harold passed away on October 20, 2007, from complications associated with a stroke he had suffered some years earlier.

One of the more bizarre episodes at the interface of Harold's personal and professional life came to light in 1978. Harold had not felt well for nearly a year, having suffered from chronic pains in his chest and down his spine, occasional dizziness, and coldness in his extremities. He had not considered an environmental cause of his illness until he learned that Malcolm Corden, another scientist on the

same floor, had suffered with similar symptoms for about the same time frame. The two professors began to consider an environmental source of their symptoms. Cordley Hall housed several departments and many active research laboratories, and they wondered whether toxic chemicals being used in some of those laboratories might be the source of their problems. They were surprised to learn that five other faculty members with offices on the same floor had experienced similar symptoms. Neurologists were not able to diagnose a specific illness associated with the symptoms both Corden and Evans experienced. A National Institute of Occupational Safety and Health team was unable to find a clear-cut relationship between the scientists' symptoms and the work environment. Nonetheless, a simple empirical experiment by Charles Leach, a plant pathologist in the department, revealed lapses in the exhaust system in the building. Fragrant mint oil released into the exhaust vents in a fourth-floor laboratory was detected by smell in professor Leach's office within 40 seconds, and within 90 seconds, the smell was detected on the first floor. Eventually the exhaust vents on the roof were raised 8 to 15 feet to ensure that exhaust was expelled vertically into open air with little or no chance of it being drawn back into the building through air intakes. With time, the symptoms went away and both men returned to normal health. A cause of the symptoms was never identified and a direct effect associated with raising the exhaust vents was not established.

SCIENTIFIC CONTRIBUTIONS

The Molybdenum Period, 1946-1958. Harold began his scientific career by investigating mineral nutrition in tobacco in his native state of Kentucky. Over the ensuing 46 years he published over 200 scientific papers concerning the biochemical role of minerals in plant nutrition and various

aspects of biological nitrogen fixation. His early work dealt with the practical issues of correct fertilizer usage on crops. He had the great foresight to realize that it was not just the big three (i.e., nitrogen, phosphorus, potassium) that controlled crop productivity but that micronutrients—in particular molybdenum and, somewhat later, cobalt—could have tremendous impact. Although Harold was best known in his late career as a champion of nitrogen fixation, he never really gave up his roots in micronutrient physiology, finding astounding and unique ways to merge the two fields.

Harold was aware of earlier observations by H. Bortels in 1930 that molybdenum was essential for nitrogen fixation by bacteria in culture. One of Harold's favorite sayings was that the path for a scientist to be successful was "to read what everyone else was reading and then think what no one else was thinking" and the molybdenum story is the first such example of this maxim that set the pattern for his remarkable career. Could Bortels's molybdenum observations be extended to nitrogen-fixing plants in the field? Harold's move to Johns Hopkins University was fortuitous because the acidic soils in nearby New Jersey were perfect candidates to examine this hypothesis. Molybdenum addition to fields of alfalfa and red clover, both nitrogen-fixing crops, did indeed provide substantial increases in productivity. The next step was to search for the underlying mechanism behind this response. This led briefly away from nitrogen fixation toward other aspects of nitrogen metabolism, specifically enzymatic conversion of nitrate to nitrite by nitrate reductase. Working with cell-free extracts of *Neurospora*, Harold demonstrated for the first time in any organism that NADPH (called TPNH at that time) and FAD were necessary for this process. Shortly thereafter he confirmed that molybdenum was associated with nitrate reduction in soybeans, the first demonstration of this essential feature in plants. Soybeans proved to be an

ideal model for such studies because both nitrogenase (the enzyme that fixes nitrogen in soybean nodules) and nitrate reductase have an absolute requirement for a molybdenum factor, albeit two different cofactors. Soybeans were well suited for biochemical studies because their nodules were much larger than those of other common nitrogen-fixing crops and thus provided more biomass for biochemical studies such as protein purification and characterization. Soybeans remained Harold's plant of choice even after he left the soybean-growing regions of the United States. His greenhouses and field plots at Oregon State University were one of the few places in the entire Pacific Northwest where soybeans could be found.

Harold continued to make a series of important contributions to the role of molybdenum and other nutrients with regards to their interactions with plant enzymes (e.g., cytochrome oxidase, cytochrome reductase, pyruvate kinase, malic enzyme, polyphenol oxidase), but his attention was about to be diverted in a startling new direction.

The Cobalt Breakthrough, 1959-1966. Cobalt is hardly an element that comes to mind as a plant nutrient, being somewhat scarce and exotic. But Harold opened new doors when he showed that cobalt was required by nitrogen-fixing bacteria (*Rhizobium*) in culture and by soybeans when grown under conditions in which they were dependent on nitrogen fixation. These experiments required a remarkable degree of fastidiousness since the amounts of cobalt required were exceedingly small and all traces of contaminants had to be scrupulously eliminated. Ordinary reagent-grade chemicals were much too impure and even the amount of cobalt present in a seed was typically sufficient to meet the requirements of the next generation. Once the requirement was demonstrated unequivocally, Harold proceeded to show that the underlying principle was based on the need for vitamin B₁₂

(cyanocobalamin) by *Rhizobium*. Plants *per se* have no direct requirement for cobalt or vitamin B₁₂, but their bacterial symbionts do. Over the course of the next decade, Harold developed the cobalt story with its multitude of implications for physiology of nitrogen fixation both in bacteria and in numerous nitrogen-fixing plants, even including a fern and the prominent nonlegume nitrogen fixer, red alder. By this time Harold was firmly focused on nitrogen fixation and anything that fixed nitrogen fell under his discerning attention. Although he mostly worked with soybeans, he examined many other potential fixers, including free-living bacteria, lichens, actinorhizal plants (nonlegumes, such as alder), rushes, grasses, marine systems, and even decaying wood.

The Nitrogenase Period, 1967-1975. The most distinctive feature of nitrogen fixation is nitrogenase, the enzyme that catalyzes the conversion of atmospheric nitrogen into ammonia. Nitrogenase proved to be extremely difficult to purify and characterize largely because it quickly becomes inactive when exposed to air. Although Harold was a firm believer in the adage that “youth is a wonderful thing, don’t waste it purifying enzymes,” he still led the efforts to do just that with a number of enzymes and eventually succeeded in obtaining the first active, cell-free extracts of nitrogenase from nodules. This breakthrough required using strictly anaerobic conditions throughout and adding materials such as polyvinylpyrrolidone (essentially powdered nylon) in extraction buffers to absorb potentially damaging phenolic compounds normally present in plant tissues. Such procedures are routine now but were revolutionary at the time of their first use. At about the same time (late 1960s) Harold also provided the first report of the use of the acetylene reduction technique to measure nitrogen fixation activity in plants. The procedure involves enclosing a nitrogen-fixing sample (e.g., plant, bacteria, cell-free extract) in a

controlled atmosphere containing acetylene gas. Nitrogenase will reduce the acetylene to ethylene, thus providing a simple, reliable, specific, and highly flexible method for measuring nitrogenase activity. The technique is now so routine as to be almost mundane and there is hardly a laboratory doing nitrogen fixation research anywhere in the world that does not utilize it routinely.

The Hydrogenase Revolution, 1977-1988. Good as it is at its job, nitrogenase seemed to be less than perfect, at least according to Harold. The enzyme always released hydrogen gas whenever it converted nitrogen into ammonia. Harold reasoned that since hydrogen contains a lot of energy that could be lost, this process must be energetically inefficient. Many nitrogen-fixing systems contain an uptake hydrogenase that recaptures this hydrogen. This action effectively also recaptures energy since the electrons stripped from the hydrogen gas are diverted to an electron transport chain to make ATP. Harold reported that many legumes lack such a hydrogen uptake mechanism and that this could be a distinct disadvantage in terms of eventual performance of the plant host. In order to convince the skeptics—there were many—Harold had to employ the emerging tools of molecular biology. This was a bit of a stretch for a biochemist whose graduate training predated Watson and Crick, but Harold recruited the requisite new talent and guided them skillfully to characterize the genetic system involved: the hydrogenase uptake genes (*Hup*). They created *Hup* mutants of *Rhizobium* that were isogenic in all other regards and showed that these mutants resulted in reduced yields in soybean. They also developed a sophisticated method for measuring hydrogenase activity and quantifying the hydrogenase uptake capacity. This proved to be a valuable tool in assessing the efficiency of different legume-*Rhizobium* pairings, which vary widely in this regard. Evidently, agricultural scientists had inadver-

tently selected against the most promising rhizobia because they did not realize the value of this trait. Continuing his long tradition of examining the role of minerals in enzyme function, Harold's group then purified hydrogenase protein from *Rhizobium* and showed that nickel and selenium were essential for activity.

Further work in Harold's lab showed that nickel is also required by the enzyme urease in soybean. This work, along with important contributions by other groups, led to the inclusion of nickel on the "official" list of nutrient requirements for higher plants, the last such nutrient to be added to the list. Whether or not this list is now truly complete must remain an eternally open question, but Harold always had his eye out for other possible candidates, even including arsenic, iodine, chromium, tungsten, vanadium, and other equally obscure elements. As usual, his inclinations proved to be on the mark, when others (Paul Bishop, a former postdoctoral fellow in Harold's lab) found that vanadium was involved in some nitrogenases.

Having shown that *Rhizobium* had an active hydrogenase system, Harold began to wonder whether such a capacity would be of any significance outside the host plant, even though *Rhizobium* does not usually fix nitrogen (or release hydrogen) under such conditions. Perhaps it could even utilize hydrogen as an energy source just as the so-called "knallgas" (literally "exploding gas") bacteria do. To the astonishment and general skepticism of the nitrogen-fixing world, this turned out to be the case. Not only could *Rhizobium* use hydrogen as a sole energy source in culture, but it could also use carbon dioxide as the sole carbon source through the action of the carbon-fixing enzyme rubisco. Other prominent scientists, notably John Postgate, flocked to his laboratory to confirm these results, which they quickly did.

By this time Harold's Laboratory for Nitrogen Fixation Research had become recognized as one of the most prestigious and productive centers for nitrogen fixation research in the world. In 1984 the International Congress on Nitrogen Fixation acknowledged this prominence by convening on Harold's doorstep in Corvallis, Oregon, despite the fact that Corvallis is a small and remote location that lacks the trappings of a traditional convention destination.

Even as Harold began to consider retirement, he never stopped pushing in the lab. His later years focused on more closely defining the role of selenium in nitrogen-fixing bacteria and plants. Spin-off projects sent his laboratory into explorations of antioxidants in nodules. It was Harold's thought that since selenium is an important antioxidant in animals through its role in glutathione peroxidases that it might have a similar role in plants. No such role for selenium could be identified, but the research did lead to the identification of ascorbic acid (vitamin C)-based antioxidants in nodules that have spawned a still vibrant field of research. Nevertheless, Harold's suspicions regarding a possible role of glutathione peroxidase in nodules were, as usual, still on point and ahead of the rest of the pack. Twenty years later others have confirmed that nodules do indeed contain their own glutathione peroxidases even though they do not have the same requirement for selenium that animal forms do.

Harold J. Evans will be remembered for his contributions to our understanding of mineral nutrition in plants and bacteria and to our understanding of how plants accumulate nitrogen for growth. Trace elements such as molybdenum, cobalt, nickel, and selenium are often present in tap water and high-purity reagents in high enough concentrations to support plant growth. So the study of their roles in plants required a careful and rigorous approach. Harold was the right person to tackle the challenge. His tenacity coupled

with his careful approach led him to make many important discoveries in the fields of mineral nutrition and plant nitrogen metabolism. In addition to his scientific contributions, Harold's legacy consists of the many professional plant scientists who trained under him as graduate students, postdoctoral scholars, and visiting scientists.

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